

*Review*

# The conservation physiology of seed dispersal

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At a time when plant species are experiencing increasing challenges from climate change, land-use change, harvesting and invasive species, dispersal has become a very important aspect of plant conservation. Seed dispersal by animals is particularly important because some animals disperse seeds to suitable sites in a directed fashion. Our review has two aims: (i) to highlight the various ways plant dispersal by animals can be affected by current anthropogenic change and (ii) to show the important role of plant and (particularly) animal physiology in shaping seed–dispersal interactions. We argue that large-bodied seed dispersers may be particularly important for plant conservation because seed dispersal of large-seeded plants is often more specialized and because large-bodied animals are targeted by human exploitation and have smaller population sizes. We further argue that more specialized seed-dispersal systems on island ecosystems might be particularly at risk from climate change both owing to small population sizes involved but also owing to the likely thermal specialization, particularly on tropical islands. More generally, the inherent vulnerability of seed-dispersal mutualisms to disruption driven by environmental change (as well as their ubiquity) demands that we continue to improve our understanding of their conservation physiology.

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## 1. INTRODUCTION: THE IMPORTANCE OF DISPERSAL AND OF ANIMAL SEED DISPERSERS

Dispersal is a fundamental life-history process allowing organisms to reduce competition among kin and to colonize new, suitable habitats. In scenarios of current global change, dispersal is a particularly important life-history stage because it determines the future ranges of organisms, i.e. whether organisms can adjust their distribution to current and future changes in their abiotic and biotic environment. This general phenomenon is illustrated by post-glacial changes in the distribution of European tree species [1]. Most animals are mobile for at least one stage of their development; by contrast, plants are essentially sessile with their only chance of dispersal being as seeds. Seeds are not self-powered and almost exclusively rely on some external agents to provide transport. Plants make extensive use of the self-powered movement of animals, as well as of abiotic agents such as air and water currents, to transport their seeds. Howe & Smallwood [2] estimated that 51–98% of canopy trees and 77–98% of sub-canopy trees and shrubs in neotropical forests attract animals as seed dispersers using fleshy fruits (i.e. fruits consisting of nutritional fruit pulp surrounding the seeds).

Dispersal of seeds away from the parent plant might have a number of selective advantages. Firstly, it might reduce the exposure of the immobile seed to predators or pathogens that are attracted to, or supported by, the parent. Furthermore, it reduces the potential for competition between parent and offspring, and among offspring. Even in the absence of these effects, there might still be selection for dispersal if this reduces the risk of the parent and offspring simultaneously experiencing similar adverse conditions. That is, dispersal may be selected by the need for spreading of risk in a spatio-temporally variable environment, where localized and unpredictable disasters can occur. These concepts have been encapsulated in the Janzen–Connell hypothesis to explain the diversity on small spatial scales in many plant communities (introduced independently by Janzen [3] and Connell [4]). This hypothesis suggests that diversity is maintained by two mechanisms: (i) mortality of seeds and seedlings increases as their density increases and (ii) survival of seeds or seedlings increases with increasing distance from the parent.

At a time when plant species are experiencing increasing challenges from climate change, land-use change, harvesting and invasive species, dispersal has become a very important aspect of plant conservation. Dispersal is particularly important because some animals disperse seeds to suitable sites in a directed fashion. Our review has two aims. Firstly, to highlight the various ways plant dispersal by animals can be affected by current anthropogenic change. Secondly, to show the important

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role of plant and (particularly) animal physiology in shaping seed–dispersal interactions.

Let us now consider what qualities make a good dispersal agent. Although an effective dispersal agent transports the seed away from the parent, there may not be selection for ever-further dispersal. Indeed, dispersal beyond a certain distance may be detrimental to fitness. Wenny [5] followed the success of bird-dispersed seeds of the tree *Beilschmiedia pendula* in Costa Rica. Those transported less than 10 m from the parent suffered high mortality through predation and fungal diseases. However, seeds transported more than 30 m had lower survival than those transported 10–20 m. This effect probably arises because the environment close to the parent is more likely to be suitable to this species than some more distant environments (because it was demonstrably suitable to the parent). That is, because seeds start out in an environment that has been successful for their parent, sites nearby the parent may be more likely to offer suitable conditions to offspring than more distant sites. The greater the homogeneous spatial scale of habitat, the less this selection pressure for limited dispersal distances will be [6]. The plant can influence seed-dispersal distances by preferential attraction of some seed dispersers over others, and by influence of the behaviour and physiology (e.g. gut passage time) of the disperser.

Another desirable property of a dispersal agent is that it transports the seed in a way that does not damage its future ability to develop into a plant. The dispersal agent should also deposit the seed in a suitable microhabitat to aid germination and increase plant viability. From the viewpoint of the plant, seed dispersers often differ in two crucial properties: (i) the distances they disperse seeds away from the parent plant and (ii) the specific microhabitats they deposit seeds, e.g. open versus covered areas [7]. Only if plants can use different microhabitats similarly, may there be selection to attract different dispersal agents to reduce between-sibling competition and as a strategy to spread risk. Given the limited knowledge on the microhabitat use of different seed dispersers, this idea remains speculative.

We next consider the involvement of aspects of an animal's physiology in shaping its effectiveness as a seed-dispersal agent. Space constraints mean that we focus here on seed transport by vertebrate frugivores and granivores. Invertebrate seed dispersers (particularly ants) are ecologically important, as can be carriage on the fur or plumage of vertebrates—these dispersal modes (as well as the general sensory physiology involved in seed dispersal) are discussed further and compared with the mode considered here in Schaefer & Ruxton [8]. We do, however, consider fleshy and dry fruits as well as seeds without any extra food reward.

## 2. LINKS BETWEEN ANIMAL PHYSIOLOGY AND DISPERSER EFFECTIVENESS

It goes without saying that seed dispersal by animals can be effective only if fruits are readily detected by animals and if the nutritional rewards provided by

them are attractive to the animals (except for dispersal by chance on the fur or plumage of animals). Consequently, an animal's sensory and digestive physiology are important determinants of the interactions among fruiting plants and animals (see §2*a*). In general, the seed or associated fruit experiences some physical pre-processing by the animal prior to ingestion. Next, it must be deposited by the animal in a viable condition (§2*b,c*). In §3, we consider how plant traits involved in interacting with animals can be under environmental control. In §4, we explain why seed dispersers are important for plant conservation before detailing in §5 how understanding animal physiology is important for the conservation of plants.

### (a) Digestive physiology of the animal and the nutritional value of seeds and fruits

The animal needs an incentive to transport the seed, and this incentive is nutritional. Much of a seed is a store of nutrients for the seedling to exploit before it can photosynthesize, hence the seed naturally represents a nutritional reward for many animals to hijack. Animals that destroy seeds to assimilate their nutrients are often termed seed predators because they can be detrimental to plant fitness. Plants have evolved secondary compounds in seeds (such as tannins) that serve to make them less attractive to would-be predators. However, seed predators are counter-selected to overcome such defences, and seed and seed predators are locked in an arms race. Interestingly, the relationship between plants and seed predators can be complex, and both defence and attraction of seed consumers can arise. This is because seed predators can also increase plant fitness through seed dispersal. Seed dispersal occurs if seed predators do not consume the seed immediately but transport it some distance before caching it for later consumption (a process often called hoarding), providing that later consumption does not occur. Caching occurs in dry fruits that do not rot quickly. It can be seen as a strategy for the seed eater to cope with seasonal or daily variation in food availability. The plant benefits from its seed being cached only if the seed can germinate before it is discovered and eaten (either by the original cacher or by a thieving granivore). The original cacher may not return to the seed if it dies beforehand, or if it forgets the location of the seed, or if it has less need for cached seeds than anticipated owing to alternative food resources. The survival rate of cached seeds is very variable. It has been estimated to be as low as 0.02 per cent in some systems [9], but has also been recorded as being as high as 10 per cent in others [10]. For example, many rodents store seeds at different locations rather than in an aggregate. While this tactic increases the cognitive, time and energy costs of retrieval, it is seen as a tactic to make searching less attractive to potential pilferers [11], as well as a spreading-of-risk strategy against pilferers, infection and natural disasters causing the loss of cached food in a specific location.

When a seed is discovered by a granivore, the key issue is whether it is eaten immediately or cached.

This decision will be influenced by many factors, some of which the plant can influence. For example, increasing simultaneous availability of seeds through masting, high nutritional value to individual seeds, hard seed coatings that take time to penetrate and secondary chemicals such as tannins that can increase seed longevity all encourage caching rather than immediate consumption (see [12] for a review). Thus, we can expect that for many seed–granivore interactions, there is complex interplay between the digestive physiology of the animal and the constitution of the seed. Paradoxically, we would not expect seeds to always be selected to minimize their attractiveness to granivores.

Fleshy fruits appear easy to exploit, they are often strong smelling and/or conspicuously coloured. After all, they are meant to be eaten in exchange for seed transport. Yet, there is the conundrum that fleshy fruits are not always as attractive as one might expect [13]. There are a number of potential answers for this. One reason is that plants need to protect their nutritious fruits against fruit predators that consume fruit pulp but do not disperse seeds. This protection is often chemical. Plants defend fruits by using secondary compounds that lower the risk of fungal infection or fruit damage by invertebrates. Often, however, the secondary compounds make fruits also less attractive to seed dispersers [14]. It is also important to remember that plants do not benefit if the frugivore remains so long on a plant that it deposits seeds under the parent. Thus, plants may be selected to offer an incomplete suite of nutrients to encourage animals to adopt a broader diet [15]; this may be taken a step further if plants include secondary compounds in fruits that are detoxified by consumption of another food type. However, maximization of foraging efficiency will encourage selection by frugivores to minimize travel between food sites and exploit each maximally, hence again we expect complex counter-selection between fruit composition and frugivore digestive physiology, such that fruits are attractive to frugivores but not quite as attractive as frugivores would like.

#### **(b) Interaction between germination and animal digestion**

It is important to acknowledge that passage of seeds through the gut influences the fraction of seeds that germinate and the distribution of germination times [16,17]. Clearly, dispersal can be costly if it reduces the likelihood of seeds germinating. Such a reduction can occur, for example, because passage through the gut can decrease the mechanical protection of seed coats [18]. However, these costs can be offset, e.g. if seeds are deposited by animals in very favourable microhabitats. Gut passage can also affect the timing of germination through the effects on seed coats. The timing of germination can be critical for plants. A meta-study revealed that early emergence generally enhances plant fitness, particularly by increasing growth and fecundity [19]. However, the effect of early emergence on plant fitness was greater under controlled conditions compared with field conditions,

presumably because many other biotic and abiotic factors decelerate seedling growth in the field. Thus, Verdú & Traveset [19] suggest that selection on emergence time will vary in time and space slowing the overall rate of evolutionary change. It is feasible that climate change can alter selection pressure on the timing of germination, and that it can also alter the costs and benefits in the interactions among plants and seed dispersers. Such effects will vary according to disperser species because these differentially influence germination time; for example, owing to differences in the degree of abrasion of seed coats or the amount of dung in which seeds are deposited [20]. It is important to stress the gap in our current knowledge on the trade-offs shaping seed–dispersal interactions that impede realistic conclusions on how climate change will affect seed–dispersal systems.

Further complication arises because plants can actively influence gut passage time. Some fruits contain secondary compounds that can act to either retard or accelerate gut passage times [21]. For example, capsaicin, the substance that makes chilli pungent, increases seed retention time in avian seed dispersers [22]. However, this constipative effect occurred only after an 80-min time lag, thereby affecting a larger proportion of fruits consumed and dispersed by large birds compared with small birds, which usually have shorter gut retention times than 80 min. However, increased gut retention times reduced germination in pungent fruits because seed coats of pungent fruits are 10–12% thinner than those of non-pungent fruits in the polymorphic species *Capsicum chacoense* [18]. Seeds with thinner coatings thus had a greater risk of abrasion through the animal's gut than seeds with thicker coating. Because fruit pulp has been demonstrated to often contain secondary compounds that can either inhibit or delay germination, and seeds of a given type can experience positive, negative or no effects when passed through different types of animals, it is not easy to predict the relative effectiveness of dispersers with different digestive physiologies. This limitation applies even more because secondary compounds may also influence the size of animals' defaecation and the density of seeds in each defaecation. These factors are important for seed dispersal because they likely influence the risk of seed predation subsequent to defaecation, competition between seedlings and seedling vigour (through fertilizer effects of the excrement itself [16]).

In some very unusual cases, germination of seeds may be possible only after passage through the digestive system of a suitable animal. Traveset [23] cites Rick & Bowman [24] as suggesting that seed dormancy in the native Galapagos tomato (*Lycopersion esculentum*) was broken only after ingestion by giant tortoises. However, even if germination can occur in the absence of suitable dispersers, these are still required to transport the seed away from the parent plant and can thereby enhance germination probability. This was found in the rewilding study by Griffiths *et al.* [25] (see §4). Consequently, resurrecting the interactions between large-bodied seed dispersers and dispersal-limited plants is an increasingly important topic for conservation biologists.

### (c) *Animal physiology and dispersal distances*

Dispersal distance will be a complex function of retention time of seeds in the digestive system, the locomotive ability of the animal and its behaviour. The retention time of seeds is affected strongly by physiology, with flying endotherms having very short retention times (typically of the order of a few minutes to a few hours) and large ectotherms having very long retention times (typically one to two weeks). However, although birds and bats might have short retention times, they can still disperse seeds over distances of hundreds of metres (and in rare cases over thousands of kilometres and entire continents [26]) because flight speeds can be very high. The relative importance of different animal taxa for long-distance seed dispersal might also vary according to habitat type. In the open woodland of southern Spain, long-distance dispersal of *Prunus mahaleb* depended particularly on mammals while birds dispersed most seeds only short distances [27]. Conversely, birds and bats achieved longer dispersal distances than mammals in a neotropical forest [28]. The transit time of seeds through the gut will vary according to properties of the seed (with small seeds having generally longer retention times). Retention of a particular seed will also be strongly influenced by gut fullness at the time of passage, the make up of other constituents of the gut, and also the recent foraging history of the animal.

### 3. ENVIRONMENTAL EFFECTS ON PLANT PHYSIOLOGY

Climate change may affect the interactions between plants and animals owing to environmental effects on plant traits that attract animals and influence their foraging decisions. Changes in the environment may affect both antagonistic interactions, such as herbivory, as well as mutualistic ones, such as pollination and seed dispersal. For example, phenols constitute a large group of secondary compounds that are under environmental control because they reduce photo-damage in plants [29]. At the same time, phenols include deterrent substances that reduce herbivory and fruit consumption by frugivores in leaves and fruits, respectively [14,30]. Given that the light-induced synthesis of phenols is 'a finely tuned process which must be explained in terms of plant physiology' [31], current climatic change may affect plant chemistry and thereby alter the interaction between plants and their seed dispersers [32]. Increasing temperature and drought are abiotic stressors that would lead to greater stress responses by plants (and elevated concentrations of some secondary compounds such as anthocyanins that mediate such stress responses [33]) which may subsequently alter the patterns of seed dispersal by animals. Currently, there are not sufficient data available to predict the direction and magnitude of such effects, but the implication for plant conservation makes these very much worthy of urgent study.

Environmental effects occur also on flower and fruit coloration. In plant species that are polymorphic for anthocyanin (a class of phenols) pigmentation, the pigmented morphs are more tolerant to environmental

stressors, such as drought and high temperatures [33]. Artificially imposed drought conditions increased the frequency of pigmented morphs in *Cirsium palustris* [34]. Such environmental effects can have two consequences on plant–animal interactions. Firstly, in *Raphanus sativus* anthocyanin-pigmented morphs are avoided by both pollinators and herbivores owing to their higher chemical defences [35]. This example illustrates our core topic in this section, i.e. that environmental effects have the potential to alter the relationship between plants and both their antagonists and mutualists. Secondly, variation in floral coloration can induce strong shifts in the pollinator species a given plant interacts with [36] because some colours may be easier to detect for pollinators than others. Consequently, environmental effects may also shift plant–animal interactions owing to their interactions with animal sensory physiology. Again, such changes are currently known from very few species and more work in this area is required in order to derive predictions on climate change.

### 4. ARE ANIMAL SEED DISPERSERS IMPORTANT TO PLANT CONSERVATION?

One of the most pervasive of anthropogenic ecological effects is habitat change and fragmentation. Dispersal mechanisms will be key to system-wide conservation of species in the face of habitat loss and fragmentation. The very large-scale study of Montoya *et al.* [37] argues that plant species with animal seed dispersers may be more robust to fragmentation than wind-dispersed species. They measured local forest cover for a given 1 × 1 km cell in Spain, and recorded the fraction of the eight neighbouring cells that were classified as being forested. The authors found that for a given tree species, its absence in a given cell was correlated with the number of neighbouring non-forested cells; however, this effect was much stronger for wind-dispersed than animal-dispersed species. Montoya *et al.* conclude from this that animal-dispersed trees may be more robust to anthropogenic habitat loss than wind-dispersed species, and that this is driven by the directed dispersal of animal dispersers towards areas of suitable habitat. These conclusions on seed dispersal by trees might not apply universally. In contrast to Montoya *et al.* [37], Alados *et al.* [38] found that vertebrate-dispersed shrubs were more susceptible to fragmentation than other shrubs. The authors postulated that the reason for this was positive feedback between the abundance of a fruiting species on a given patch and the ability of that patch to attract appropriate animal seed dispersers (i.e. fruit tracking by frugivores).

While fragmentation is thought to decrease seed dispersal for most plant species, some animal-dispersed species may benefit from fragmentation if this increases the amount of edge-habitat that is particularly attractive to their seed-dispersers [39]. However, the ecology of seed dispersal on habitat edges is complex, and generalization across habitats is difficult [40]. Furthermore, connective corridors between patches of a fragmented population may be less important to avian-dispersed species than



mammalian seed-dispersing species [41]. However, corridors can still have positive effects on avian seed dispersers although (as with edge effects) the underlying mechanisms can be complex. Levey *et al.* [39] demonstrated that corridors between patches of regenerating vegetation in a mature pine forest enhanced seed dispersal of the wax myrtle (*Myrica cerifera*) by eastern bluebirds (*Sialia sialis*) even though birds never flew along the corridors. Careful observation revealed that birds preferred to fly long distances between fragments through the forest rather than along the corridors; however, they were strongly attracted to following edges, and corridors provided edges that led them from one patch to another.

It is important to remember that anthropogenic changes can affect animal-dispersed plants through various adverse effects on the animal mutualists (e.g. hunting, loss of breeding sites and loss of other food sources). A very convincing demonstration of the effect of frugivore loss on tree recruitment is the large-scale manipulative experiment of Wotton & Kelly [42]. They found that recruitment of two large-seeded trees was reduced by dispersal failure and by introduced mammalian seed predators, and that these effects were synergistic. Large-seeded plants may be more vulnerable to loss of a particular frugivorous species because their larger fruits can be consumed by fewer animals, and large animals are often the target of hunters. Dispersal of seeds from the two focal tree species in this study appears almost completely reliant on one species: the New Zealand pigeon (*Hemiphaga novaeseelandiae*). This reliance itself likely has human-derived origins: 41 per cent of endemic forest bird species have been driven extinct since human settlement of New Zealand (with extinctions being biased towards large-bodied species). The pigeon itself has seen a dramatic fall in numbers and is still subject to high levels of nest predation by introduced mammals and illegal human hunting. Hence, here we have a case where introduced mammals (mainly ship rats and possums) have had an adverse effect on seed dispersal both directly through seed predation, and indirectly through competition with and predation upon seed dispersers. Similarly, Lefevre & Rodd [43] report that human-disturbed tropical rainforest held a substantially different suite of avian seed-dispersing species than nearby unaltered sites, and that this affected the types of fruits consumed. Cordeiro & Howe [44] investigated 80-year old forest fragments in Tanzania. They found that recruitment of seedlings of animal-dispersed tree species was three times greater in continuous forest and large forest fragments (less than 30 ha) than in small fragments (more than 9 ha), which they linked to a strong trend of decreasing primate and bird densities with fragment size. Similar effects were found by Cordeiro & Howe [45] for the endemic tree *Leptonychia usambarensis* in Tanzania. Birds that dispersed *L. usambarensis* seeds in continuous forest were rare or absent from small fragments, where in turn seedlings established closer to their parent and in denser aggregations. Again, this tree may be especially vulnerable because of its relatively large seed size (11 cm length).

A final line of evidence of the importance of avian seed dispersers for plant conservation comes from

manipulative studies where enhanced seed abundance and species richness have been demonstrated upon experimental provisioning of perches. This was demonstrated in regenerating *Araucaria* forest in Brazil by Zanini & Ganade [46], and in restoration of forests after landslides in Puerto Rico by Shiels & Walker [47].

## 5. LINKING PLANT CONSERVATION TO THE PHYSIOLOGY OF DISPERSERS

### (a) *Islands might be particularly vulnerable to breakage of seed-dispersal mutualisms*

Clearly if animals play an important role in the conservation of plant species, then plants may be vulnerable to decline in (or extinction of) those animals. There is good evidence of this from flying foxes (pteropid fruit bats). These are particularly important dispersers of large seeds on tropical Pacific islands, because non-flying large vertebrates are often absent and avian species have gone extinct in recent centuries. McConkey & Drake [48] demonstrate a strong non-linear relationship between the density of flying foxes and seed dispersal away from the parent tree. They hypothesize that this is driven by fruit kleptoparasitism at high bat densities. When densities are low, a bat will typically remain on one tree for long periods, collecting large-seeded fruit and carrying each in its mouth to a suitable perch (often in the same tree) where the fruit is dismembered and the seeds discarded. However, when bat density is higher 'sneaker' bats will land in a fruiting tree and take a fruit, only to be chased away by the resident bat. This 'sneaker' will thus tend to carry fruit further before dismembering them, will sometimes drop fruit during its escape flight from the resident, and will generally exploit a number of different trees in succession. The importance of flying foxes as seed dispersers comes in large part from aspects of their physiology: flight allows them to routinely transport seeds over large distances, and their large size (sometimes with wingspans approaching 2 m) allows large fruit to be carried. However, they face strong mortality from humans, being hunted for sport and food, sold commercially as a luxury food item, and killed by farmers protecting fruit trees [49]. Some flying fox species have already been driven extinct by humans.

Island ecosystems are particularly prone to species extinction, with high levels of endemism meaning that local extinction can result in the complete global loss of a species. Even when this is not the case, recolonization (without human aid) may be unlikely on human timescales. Large-seeded plants may be particularly at risk from extinction of a seed-dispersing mutualist for a number of reasons. Firstly, there is often lower species diversity on islands, leading to increased reliance on one or very few particular mutualistic animal species. Secondly, the larger the plant's seeds, the fewer animal species will be large enough to disperse them. Thirdly, dispersers of large body size are characterized by low population density and thus increased extinction risk. Finally, human-induced population decreases and local as well as global extinctions seem particularly biased

towards larger bodied animal species (see [50] for an overview). Hunting may eliminate seed dispersers; this situation has been coined as the empty forest [51], where plant diversity is still high but expected to decline owing to dispersal limitations. Not only in mammals are extinction risks biased towards large species. In birds, for example, global extinction is influenced by body mass, and some functional groups such as frugivores are particularly extinction prone [52]. Hence, if plant species suffer catastrophic seed-dispersal failure as a result of extinction of an animal seed disperser, then our expectation would be that such plants will mainly be large-seeded plants on islands. An interesting case study in this regard is the critically endangered large-fruited ebony *Diospyros egrettarum*, which is endemic to a 25-ha island off Mauritius (Ile aux Aigrettes). Intensive study of the species from 1986 to 2000 found seedlings to occur only under maternal trees [25]. This situation has been linked to the extinction of endemic *Cylindraspis* tortoises on Mauritian islands by humans in the mid-nineteenth century (within the lifetime of adult trees present now). Griffiths *et al.* [25] report on a rewilding experiment where exotic Aldabra giant tortoises were introduced onto the island so that they could disperse the ebony's seeds. The introduced tortoises ingest the large fruits of this tree and have been demonstrated to disperse large numbers of seeds, with gut passage improving germination rates and successful seedling establishment away from the vicinity of parent trees.

Such rewilding projects are highly controversial and some conservation biologists are firmly opposed to them [53]. It is certainly true that deliberate release of alien species into fragile island habitats for conservation purposes has very real potential to be spectacularly counterproductive and should be attempted only after very careful consideration, if at all. However, here we have an example where reintroduction of the historical seed dispersers of the focal tree is simply impossible, and thus the only other means of providing seed dispersal would be by employing humans as dispersers. This too is not without its potential risks to conservation and would require ongoing and substantial financial investment. Further, giant tortoises have large adult size and low reproductive rate. This implies that if the rewilding project is unsuccessful or counterproductive, removal of the entire population would be relatively easy. Moreover, their long lifespan means that it might be possible to initially introduce one sex only, and have several years monitoring the success of these individuals before the other sex is introduced and the population is allowed to expand. Rewilding much more mobile and fecund bat, bird or primate dispersers would be much less easy to both monitor and if necessary reverse. Alien tortoises have previously been introduced to other Indian Ocean islands as surrogates for extinct species, apparently without adverse effects, and in the case of Round Island have been implicated in the dispersal of seeds from previously dispersal-limited endemic trees [25].

Animal seed dispersal may be particularly important for island plants. Kaiser-Bunbury *et al.* [54] report that in New Zealand 70 per cent of woody

species produce fleshy fruits, compared with global averages of 39 per cent for temporal mainland forest, 39 per cent for Mediterranean scrubland and 46 per cent for Neotropical dry forest. It may be that directed dispersal provided by animal dispersers is more valuable in spatially restricted settings such as an island. Exploration of the relative occurrence of fruiting species on oceanic islands would be very instructive. We predict that not only will fleshy plants be more common on islands, but their prevalence should be negatively correlated with island size (because directed dispersal should become more and more valuable on smaller and smaller islands).

Lizards are particularly important seed dispersers on tropical islands. This may come about because of the low food requirements of their ectothermic metabolism. Firstly, this may increase their chance of surviving a long period at sea (compared with endothermic mammals) having been inadvertently swept to sea by flood or tsunami. Secondly, this may allow a small island to offer sufficient food to support a viable population of reptiles but not mammals or birds [55]. These authors also suggest that low arthropod densities on islands have led to selection for dietary broadening in lizards from their primarily insectivorous diet. However, the same ectothermic metabolism that has allowed lizards to be important seed dispersers on tropical islands may threaten the long-term persistence of such mutualisms. Tewksbury *et al.* [18] argue that tropical ectotherms are generally thermal specialists, with limited acclimation abilities because they have evolved in relatively constant aseasonal environments. The authors further argue that this may leave them vulnerable to climate change. This is an issue worthy of urgent research, and a critical aspect will be the scope for evolutionary change in lizard populations and the predicted timescale and magnitude of climate change predicted for different islands. We predict that narrow heat tolerance may also affect many plant species in tropical mountains such as the Andes where they have very limited altitudinal distribution.

#### (b) *Acknowledging ecosystem complexity*

It is important to remember that preservation of a seed-dispersal mutualism is not simply about protecting or reintroducing a suitable disperser. Seed-dispersal mutualisms are often embedded in a complex network of interactions involving (for example) florivorous animals that reduce seed set, animals that are attracted to the fruit but do not disperse the seeds, and animals that prey on the dispersers. Consequently, changes in the abundance of each of these animals can influence the relative dispersal success of a given plant species. This deceptively simple statement has two important implications. Firstly, it appears likely that global change will affect plant dispersal either directly (see above) or through indirect effects on the relative abundance of plant mutualists and antagonists. Secondly, indirect effects will be difficult to generalize across species because each plant species has a different network of interacting animal, fungal and bacterial species that consume fruits.

Some basic predictions can still be made. The network structure will change as some species react more quickly to global change than others. They will thus interact with species that they have not been interacting with before (e.g. because of range shifts or range expansions). Moreover, Kissling *et al.* [56] show that species occurrence and abundance will be influenced strongly by the group that react slowest to global change. They analysed species-richness data from 1005 breeding bird and 1417 woody plant species in Kenya, and found that bird species richness is expected to rise under various climate change scenarios throughout Kenya if woody plants (which provide cover and food) react as quickly to climate change as birds do. If plants responses were delayed in the models, a realistic assumption owing to the longer generation times of woody plants, there is a reversed trend of reduced bird species richness under various climate change scenarios. This analysis highlights the importance of incorporating the responses of interacting species into global change models rather than focusing on distinct groups such as plants and birds separately.

Another prediction is that climate change is altering the phenologies of interacting species and that such shifts will be disparate on distinct groups. For example, black elder (*Sambucus nigra*) is a keystone species providing a fruit resource for many frugivorous animals throughout late summer in Central Europe [57]. It is a staple food for many migratory birds that can substantially increase their lipid reserves by consuming black elder [58]. The fruit ripening of black elder was strongly ( $r^2 = 0.74$ ) predicted by summer temperature (April–June) and advances 6.5 days per 1°C rise during that period [59]. Crucially, however, long-distance migrants such as the garden warbler (*Sylvia borin*) that also disperse black elder seeds show relatively low phenotypic plasticity in response to environmental conditions in their migratory schedules compared to its sister species, the short-distance migrating blackcap (*Sylvia atricapilla*) [60]. As such, the overlap in the phenologies of fruiting black elder trees and long-distance migrants as seed dispersers may change more drastically than the overlap with short-distance migrants as seed dispersers.

Mutualisms can be affected by other plants that may compete for the attention of seed-dispersing animals, and by invertebrate animals, fungi and other micro-organisms that can exploit fleshy fruits and in so doing make them less attractive to dispersers. For example, decreases in large-bodied seed dispersers may reduce the competitive edge of large-seeded species compared with plants with smaller seeds that are dispersed by smaller-bodied animals in climax habitats. At the same time, seed predators are smaller and less likely to be hunted in Southeast Asian forests than seed-dispersing animals [61]. Thus, hunting by humans can change the patterns of seed dispersal by animals in various ways and thereby drive changes in vegetation structure [50]. Owing to such indirect effect, the conservation measures to protect a specific seed-dispersal mutualism may involve control of other species. As an example consider the blue-tailed day-gecko *Phelsuma cepedianana* that is endemic to Mauritius and is currently the sole pollinator and

seed disperser of the critically endemic plant *Roussea simplex* [62]. Fewer than 100 plant individuals exist. The flowers and fruit of this plant are exploited by the invasive ant *Technomyrmex albipes*, which feeds on the nectar and on fruit pulp and reacts aggressively to disturbance on the plant by any approaching animal, including the gecko. Hansen & Müller [62] demonstrate that gecko visitation rates were considerably higher at flowers and fruits of plants from which ants had been experimentally removed and excluded. Indeed, they report that in their experiments geckos never approached ant-infested plants unless ant density was unusually low. Intervention to improve seed dispersal by geckos is likely to be very challenging. Broad-scale control of the ants seems impossible, and thus the only feasible alternative might be to routinely remove and exclude them from individual plants. The experiments of Hansen & Müller [62] suggest that such intervention could significantly improve the seed dispersal of this species, but such a conservation undertaking would be labour (and thus cash) intensive.

The complexity of seed-dispersal mutualisms and the challenges that this raises for conservationists can be illustrated by seed dispersal in Hawaiian rainforests. Foster & Robinson [63] argue that the Hawaiian Islands have lost nearly all their native seed dispersers to extinction but have gained a number of frugivorous birds through introductions. These introduced birds are not only the dominant or sole dispersal agents for many native plants but have also been implicated in the reestablishment of six native understory plant species. However, the flip side of this is that these same avian species have been just as heavily implicated in the spread of a number of invasive plants. Hence, the introduced birds can be seen as very much a double-edged sword in the conservation of Hawaiian rainforests, and the dilemma for conservationists in this regard can be linked to frugivore digestive physiology. In comparison to plant pollinators, specialism is less common in seed dispersers. This has been a conservation boon in the case of the introduced giant tortoises discussed earlier, but not so in the case of the introduced Hawaiian birds because they feed on and disperse both native and invasive plants.

### **(c) *The prime importance (and complexity) of animal physiology to dispersal function***

Giant tortoises also demonstrate that what makes a species a suitable agent for introduction as a seed disperser can be a complex mix of different physiological traits. Experiments with giant Aldabran tortoises show that they might be suitable surrogate dispersers for the critically endangered Mauritian endemic plant *Syzygium mamillatum*. Hansen *et al.* [64] demonstrated that (unusually) separation of the seeds from the fruit flesh reduces germination rates of seeds, and such separation occurs during passage through a tortoise. However, they conclude that despite this cost, tortoises still offered a net benefit in seedling establishment because they removed seeds from the vicinity of parent plants (often to considerable distances away, since gut passage times were of the order of three to four weeks), and because



deposition in dung provided a nutrient supply to the seedling. This was seen as particularly valuable in a situation where much of the potential range of this plant has been adversely affected by heavy soil erosion. Conservation concerns relating to seed dispersal certainly extends beyond island ecosystems. Anderson *et al.* [57] argue that fish are important seed dispersers in the Amazonian basin, but that this ecosystem service is being substantially weakened by overfishing. They focus particularly on the large-bodied characid, *Colossoma macropomum*, local populations of which have fallen by as much as 90 per cent in recent decades. They argue that fish are very important dispersal agents because they provide directed dispersal towards suitable sites on the extensive seasonally flooded area. By contrast, wind and terrestrial vertebrates (such as birds and primates) will disperse many seeds to locations that never flood and thus do not receive the seasonal input of nutrients provided by floodwaters and necessary for many plants to flourish. Furthermore, in contrast to water-borne dispersal of buoyant fruit, fish can transport seeds upstream and between different tributaries. Estimated dispersal distances by fishes are relatively long, with 5 per cent of seeds projected to disperse 1700–2110 m from the parent plant. This is associated with the low ectothermic metabolism of the fish producing long seed retention times in the gut (of the order of 6–7 days), combined with relatively wide-ranging and fast travel compared with terrestrial ectothermic vertebrates, and rapid changes in available habitat owing to the seasonal nature of floodwaters. However, the negative impacts of overfishing on dispersal extend beyond simple reduction in numbers of dispersers. Firstly, overfishing has led to a dramatic change in the size structure of the fish population, with increasing bias towards small individual size. This is significant because seed retention times and thus dispersal distances increase with individual body size. Further, when local population densities are high, fish rapidly exhaust the fruits available from one source plant and move on to another. Such high movement rates increase the dispersal distances of seeds and increase the chance of seeds being deposited away from the parent plant. Conversely, when local fish density is low, a given individual will remain longer in the vicinity of a given fruiting plant, and its effectiveness as a disperser is thus reduced.

The Balearic islands in the western Mediterranean Sea offer another illuminating system, because historically endemic lizards of the genus *Podarcis* have been important seed dispersers, but these have been driven extinct in some islands by introduced mammalian carnivores, at least one of which (the pine martin *Martes martes*) is also an important frugivore [65]. Dispersal success of the native scrub species *Cneorum tricoccon* decreases significantly on islands without lizards. The effectiveness of the lizards is a little surprising at first, because they are territorial, thus reducing dispersal distances, are small-bodied and so have a short digestive time for an ectotherm (2–3 days), and also preferentially select small fruits that have small seeds. However, there appear to be counterbalancing advantages of lizard-based dispersal. Traveset & Riera [66] argue that seed predation is lower for lizard-dispersed seeds both because the

seeds are encased in faeces for a time, and because dispersed seeds are at lower density than those under a parent tree and so are less likely to attract the attention of seed predators. More interestingly yet, seedlings of the obligate lizard-dispersed scrub *Daphne rodriguezii* on Menorca survive better when growing under vegetation than when growing in the open (presumably because of the heat stress and water loss associated with direct and strong illumination). Lizards habitually shelter from sun and predators under vegetation and so preferentially disperse seeds to suitable microsites.

#### **(d) Can we use dispersers to control invasive plants?**

Gosper *et al.* [67] argue for consideration of modification of disperser behaviour for control of invasive plant species. They suggest exploration of chemical spraying of fruits to make them aversive, addition of perches for birds or dense vegetation patches for mammals as a way of concentrating seed deposition, provision of alternative food to discourage uptake of fruit from the focal invasive type and creation of dispersal ‘barrier zones’ with systematic removal of plants attractive to the relevant dispersal agent over an area sufficiently wide to substantially reduce seed transport across the zone. All of these interventions strike us as requiring recurrent large-scale investment of human resources. Our feeling is that such investment might more effectively be targeted at destruction of the unwanted plants themselves rather than behavioural modification of dispersers. The diet generality of dispersers suggests that effects of the suggested interventions on non-target plant species may be difficult to predict and potentially detrimental.

#### **(e) Can seed dispersal contribute to conservation of endangered animal species?**

While there seems to be a number of situations where frugivores are critical to conservation of endangered plant species, we know of only one situation where the reverse is true, that is where fruiting plants are critical to the conservation of endangered animal species. This asymmetry occurs because some plant species (especially island endemics with large seeds) can become dependent on a single disperser species. However, the dependency of animals on specific plants does not seem true, at least in part because plants generally produce only fruit at discrete intervals and the animal must be sufficiently generalist to support itself in the periods between. The closest example we have is New Zealand’s critically endangered nocturnal parrot, the kakapo (*Strigops habroptilus*), whose population at the time of writing is estimated at 131. This species only breeds in years of local masting of fruit trees, especially the rimu (*Dacrydium cupressium*) which masts every 3–5 years. Despite the adults having a broader diet, chicks are fed almost exclusively rimu fruit [68], and so manipulation of the local vegetation to provide reduced annual variation in fruit crop may not encourage better kakapo reproduction, and indeed may be detrimental if (as seems likely) increased plant variety comes at the expense of reduced rimu density. This is not to say, however, that frugivore biodiversity and food plant



biodiversity are unconnected; indeed a very careful study by Kissling *et al.* [69] demonstrated that avian frugivore richness in sub-Saharan Africa was strongly predicted by food plant diversity (specifically species richness of *Ficus*), and this effect remained even when climate and habitat heterogeneity were controlled for. However, the mechanisms driving this link are not yet clear, and it may even be that it is frugivore diversity that provides the dispersal services needed to sustain fig diversity rather than the other way around. A deeper understanding of these broad-scale processes would be very useful in helping set a conservation agenda.

## 6. CONCLUSION

The study of physiology should provide a vital mechanistic link between environmental change and ecological consequences [70]. Here, we have demonstrated the complexity of seed dispersal and argued that seed dispersal depends strongly on the physiology of animals, and on complex interactions among distinct plant mutualists and plant antagonists. We have further argued that there are several links on how current anthropogenic change may affect seed-dispersal systems. Despite the complexities involved, some general conclusions can be seen. Firstly, we argue that large-bodied seed dispersers may be particularly important for plant conservation because seed dispersal of large-seeded plants is often more specialized, and because large-bodied animals are targeted by human exploitation and have smaller population sizes. Secondly, we argue that more specialized seed-dispersal systems on island ecosystems might be particularly at risk from climate change owing to both small population sizes involved and also the likely thermal specialization, particularly on tropical islands. Furthermore, many island species are endemic, making local extinctions all the more serious. This importance of isolated population and dispersal between them emerges from other papers in this theme issue [71,72]. From this perspective, we argue that deliberate reintroduction of surrogate seed dispersers after anthropogenic loss of an important seed-dispersing species should not be prematurely discarded as a conservation tool, but rather should be subject to careful research and independent monitoring of existing examples. However, prevention of further extinctions must be preferred to rewilding, and an increased understanding of the role of animal physiology in shaping the effectiveness of seed dispersers should help in identifying conservation priorities. At a time when plant species globally are experiencing challenge from climate change, land-use change, harvesting and invasive species, animal seed dispersers are a very important aspect of plant conservation because some animals disperse seeds to suitable sites in a directed fashion. We face difficult decisions about how best to meet our global conservation objectives, as evidenced by current hot debate on rewilding. A strong scientific understanding of the proximate functioning of plant–animal mutualisms should increase the fraction of good decisions made. Here, we have focused on the interplay of animal physiology and seed traits, and demonstrated both the complexity of such interactions (highlighting the limits of current knowledge)

and the power of such interactions to influence plant ecology. For both these reasons, increased study into these interactions should be a priority.

Mutualism requires integration of particular features of plant and animal vectors, and compatibility between the two parties may be easily upset owing to time lags in evolutionary responses. As a result, mutualisms are particularly at risk from climate change (see Kissling *et al.* [56]) because they involve compatibility between two parties. If temperature rises, for example, then this will change the selective regimes on both parties, and may drive a range of physiological changes in both plants and animals. These changes will often influence the seed-dispersal mutualism. Here, we have argued that plant and animal physiologies are a further possible source for disrupting mutualistic interactions. It seems generally more likely that responses to global change occurring in the two parties will disrupt mutualism, rather than having a beneficial or neutral effect. Another emergent conclusion from this theme issue is the role of physiology in mediating effects of environmental change on complex interactions between species [73,74]. The inherent vulnerability of seed-dispersal mutualisms as well as their ubiquity demands that we continue to improve our understanding of their conservation physiology.

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## REFERENCES

- Clark, D. B., Clark, D. A. & Read, J. M. 1998 Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. *J. Ecol.* **86**, 101–112. (doi:10.1046/j.1365-2745.1998.00238.x)
- Howe, H. F. & Smallwood, J. 1982 Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.* **13**, 201–228. (doi:10.1146/annurev.es.13.110182.001221)
- Janzen, D. H. 1970 Herbivores and number of tree species in tropical forests. *Am. Nat.* **104**, 501–528. (doi:10.1086/282687)
- Connell, J. H. 1971 On the role of natural enemies in preventing exclusion in some marine animals and in rain forest trees. In *Dynamics of populations* (eds P. J. de Boer & G. R. Gradwell), pp. 298–312. Wageningen, The Netherlands: Centre for Agricultural Publishing and Documentation.
- Wenny, D. G. 2000 Seed dispersal, seed predation and seedling recruitment of a neotropical mountain tree. *Ecol. Monogr.* **70**, 331–351. (doi:10.1890/0012-9615(2000)070[0331:SDSPAS]2.0.CO;2)
- Cousens, R., Wiegand, T. & Taghizadeh, M. 2008 Small-scale spatial structure within patterns of seed dispersal. *Oecologia* **158**, 437–438. (doi:10.1007/s00442-008-1150-7)
- Jordano, P. & Schupp, E. W. 2000 Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecol. Monogr.* **70**, 591–615.
- Schaefer, H. M. & Ruxton, G. D. 2011 *Plant–animal communication*. Oxford, UK: Oxford University Press.
- McAdoo, J. K., Evans, C. C., Roundy, B. A., Young, J. A. & Evans, R. A. 1983 Influence of heteromyid rodents on *Oryzopsis hymenoides* germination. *J. Range Manag.* **36**, 61–64. (doi:10.2307/3897984)
- Forget, P. M. 1992 Seed removal and seed fate in *Gustavia superb* (Lecythidaceae). *Biotropica* **24**, 408–414. (doi:10.2307/2388611)

- 11 Male, L. H. & Smulders, T. V. 2007 Hyperdispersed cache distributions reduce pilferage: a field study. *Anim. Behav.* **73**, 717–726. (doi:10.1016/j.anbehav.2006.06.017)
- 12 Vander Wall, S. B. 2010 How plants manipulate the scatter-hording behaviour of seed-dispersing animals. *Phil. Trans. R. Soc. B* **365**, 989–997. (doi:10.1098/rstb.2009.0205)
- 13 Levey, D. J. & Martinez Del Rio, C. 2001 It takes guts (and more) to eat fruit: lessons from avian nutritional ecology. *Auk* **118**, 819–831. (doi:10.1642/0004-8038(2001)118[0819:ITGAMT]2.0.CO;2)
- 14 Cazetta, E., Schaefer, H. M. & Galetti, M. 2008 Does attraction to frugivores or defense against pathogens shape fruit pulp composition? *Oecologia* **155**, 277–286. (doi:10.1007/s00442-007-0917-6)
- 15 Whelan, C. J., Schmidt, K. A., Steele, B. B., Quinn, W. J. & Dilger, S. 1998 Are bird-consumed fruits complementary resources? *Oikos* **83**, 195–205. (doi:10.2307/3546561)
- 16 Robertson, A. W., Trass, A., Ladley, J. J. & Kelly, D. 2006 Assessing the benefits of frugivory for seed germination: the importance of the deinhibition effect. *Funct. Ecol.* **20**, 58–66. (doi:10.1111/j.1365-2435.2005.01057.x)
- 17 Samuels, I. A. & Levey, D. J. 2005 Effects of gut passage on seed germination: do experiments answer the questions they ask? *Funct. Ecol.* **19**, 365–368. (doi:10.1111/j.1365-2435.2005.00973.x)
- 18 Tewksbury, J. J., Levey, D. J., Huizinga, M., Haak, D. C. & Traveset, A. 2008 Costs and benefits of capsaicin-mediated control of gut retention in dispersers of wild chillies. *Ecology* **89**, 107–117. (doi:10.1890/07-0445.1)
- 19 Verdú, M. & Traveset, A. 2005 Early emergence enhances plant fitness: a phylogenetically controlled meta-analysis. *Ecology* **86**, 1385–1394. (doi:10.1890/04-1647)
- 20 Rodríguez-Péres, J., Riera, N. & Traveset, A. 2005 Effect of seed passage through birds and lizards on emergence rate of Mediterranean species: differences between natural and controlled conditions. *Funct. Ecol.* **19**, 699–706. (doi:10.1111/j.0269-8463.2005.00971.x)
- 21 Wajah, S. A., Levey, D. J., Sanders, A. K. & Cipollini, M. L. 1998 Control of gut retention time by secondary metabolites in ripe solanum fruits. *Ecology* **79**, 2309–2319.
- 22 Tewksbury, J. J., Huey, R. B. & Deutsch, C. A. 2008 Putting the heat on tropical animals. *Science* **320**, 1296–1297. (doi:10.1126/science.1159328)
- 23 Traveset, A. 1999 The importance of mutualisms for biodiversity conservation in insular ecosystems. *Rev. Chilena Hist. Nat.* **72**, 527–538.
- 24 Rick, C. M. & Bowman, R. I. 1961 Galapagos tomatoes and tortoises. *Evolution* **15**, 407–417. (doi:10.2307/2406309)
- 25 Griffiths, C. J., Hansen, D. M., Jones, C. G., Zuel, N. & Harris, S. 2011 Resurrecting extant interactions with extant substitutes. *Curr. Biol.* **21**, 762–765. (doi:10.1016/j.cub.2011.03.042)
- 26 Popp, M., Mirré, V. & Brochmann, C. 2011 A single Mid-Pleistocene long-distance dispersal by a bird can explain the extreme bipolar disjunction in crowberries (*Empetrum*). *Proc. Natl Acad. Sci. USA* **108**, 6520–6525. (doi:10.1073/pnas.1012249108)
- 27 Jordano, P., Garcia, C., Godoy, J. A. & Garcia-Castano, J. L. 2007 Differential contribution of frugivores to complex seed dispersal patterns. *Proc. Natl Acad. Sci. USA* **104**, 3278–3282. (doi:10.1073/pnas.0606793104)
- 28 Seidler, T. G. & Plotkin, J. B. 2006 Seed dispersal and spatial pattern in tropical plants. *PLoS Biol.* **4**, 2132–2137. (doi:10.1371/journal.pbio.0040344)
- 29 Close, D. C. & McArthur, C. 2002 Rethinking the role of many plant phenolics: protection from photodamage not herbivores? *Oikos* **99**, 166–172. (doi:10.1034/j.1600-0706.2002.990117.x)
- 30 Schaefer, H. M., Schmidt, V. & Winkler, H. 2003 Testing the defence trade-off hypothesis: how contents of nutrients and secondary compounds affect fruit removal. *Oikos* **102**, 318–328. (doi:10.1034/j.1600-0706.2003.11796.x)
- 31 Mole, S., Ross, J. A. M. & Waterman, P. G. 1988 Light-induced variation in phenolic levels in foliage of rain-forest plants I. Chemical changes. *J. Chem. Ecol.* **14**, 1–21. (doi:10.1007/BF01022527)
- 32 Cipollini, M. L., Paulk, E., Mink, K., Vaughn, K. & Fischer, T. 2004 Defense tradeoffs in fleshy fruits: effects of resource variation on growth, reproduction and fruit secondary chemistry in *Solanum carolinense*. *J. Chem. Ecol.* **30**, 1–17. (doi:10.1023/B:JOEC.0000013179.45661.68)
- 33 Strauss, S. Y. & Whittall, J. B. 2006 Non-pollinator agents of selection on floral traits. In *Ecology and evolution of flowers* (eds L. D. Harder & S. C. H. Barrett), pp. 120–138. Oxford, UK: Oxford University Press.
- 34 Warren, J. & Mackenzie, S. 2001 Why are all colour combinations not equally represented as flower colour polymorphisms? *New Phytol.* **151**, 237–241. (doi:10.1046/j.1469-8137.2001.00159.x)
- 35 Irwin, R. E., Strauss, S. Y., Storz, S., Emerson, A. & Guibert, G. 2003 The role of herbivores in the maintenance of a flower color polymorphism in wild radish. *Ecology* **84**, 1733–1743. (doi:10.1890/0012-9658(2003)084[1733:TROHIT]2.0.CO;2)
- 36 Bradshaw, H. D. & Schemske, W. 2003 Allele substitution at a flower colour locus produces a pollinator shift in monkeyflowers. *Nature* **426**, 176–178. (doi:10.1038/nature02106)
- 37 Montoya, D., Zavala, M. A., Rodriguez, M. A. & Purves, D. W. 2008 Animal versus wind dispersal and the robustness of tree species to deforestation. *Science* **320**, 1502–1504. (doi:10.1126/science.1158404)
- 38 Alados, C. I., Navarro, T., Komac, B., Pascual, V. & Rietkerk, M. 2010 Dispersal abilities and spatial patterns in fragmented landscapes. *Biol. J. Linn. Soc.* **100**, 935–947. (doi:10.1111/j.1095-8312.2010.01465.x)
- 39 Levey, D. J., Bolker, B. M., Tewksbury, J. J., Sargent, S. & Haddad, N. M. 2005 Effects of landscape corridors on seed dispersal by birds. *Science* **309**, 146–148. (doi:10.1126/science.1111479)
- 40 Restrepo, C., Gomez, N. & Heredia, S. 1999 Anthropogenic edges, treefall gaps, and fruit–frugivore interactions in a neotropical Montane forest. *Ecology* **80**, 668–685.
- 41 Damschen, E. I., Brudvig, L. A., Haddad, N. M., Levey, D. J., Orrock, J. L. & Tewksbury, J. J. 2008 The movement ecology and dynamics of plant communities in fragmented landscapes. *Proc. Natl Acad. Sci. USA* **105**, 19 078–19 083. (doi:10.1073/pnas.0802037105)
- 42 Wotton, D. M. & Kelly, D. 2011 Frugivore loss limits recruitment of large-seeded trees. *Proc. R. Soc. B* **278**, 3345–3354. (doi:10.1098/rspb.2011.0185)
- 43 Lefevre, K. L. & Rodd, F. H. 2009 How human disturbance of tropical rainforest can influence avian fruit removal? *Oikos* **118**, 1405–1415. (doi:10.1111/j.1600-0706.2009.17245.x)
- 44 Cordeiro, N. J. & Howe, H. F. 2001 Low recruitment of trees dispersed by animals in African forest fragments. *Conserv. Biol.* **15**, 1733–1741. (doi:10.1046/j.1523-1739.2001.99579.x)
- 45 Cordeiro, N. J. & Howe, H. F. 2003 Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proc. Natl Acad. Sci. USA* **100**, 14 052–14 056. (doi:10.1073/pnas.2331023100)

- 46 Zanini, L. & Ganade, G. 2005 Restoration of Araucaria forest: the role of perches, pioneer vegetation and soil fertility. *Restor. Ecol.* **13**, 507–514. (doi:10.1111/j.1526-100X.2005.00063.x)
- 47 Shiels, A. B. & Walker, L. R. 2003 Bird perches increase forest seeds on Puerto Rican landslides. *Restor. Ecol.* **11**, 457–465. (doi:10.1046/j.1526-100X.2003.rec0269.x)
- 48 McConkey, K. M. & Drake, D. R. 2006 Flying foxes cease to function as seed dispersers long before they become rare. *Ecology* **87**, 271–276. (doi:10.1890/05-0386)
- 49 Fujita, M.S. & Tuttle, M. D. 1991 Flying foxes (Chiroptera, Pterodidae): threatened animals of key ecological and economic importance. *Conserv. Biol.* **5**, 455–463. (doi:10.1111/j.1523-1739.1991.tb00352.x)
- 50 Wright, S. J., Stoner, K. E., Beckmann, N., Corlett, R. T., Dirzo, R., Muller-Landau, H. C., Nunez-Iturri, G., Peres, C. A. & Wang, B. C. 2005 The plight of large animals in tropical forests and the consequences for plant regeneration. *Biotropica* **39**, 289–291. (doi:10.1111/j.1744-7429.2007.00293.x)
- 51 Redford, K. H. 1992 The empty forest. *Bioscience* **42**, 412–422. (doi:10.2307/1311860)
- 52 Sekercioglu, C. H., Daily, G. C. & Ehrlich, P. R. 2004 Ecosystem consequences of bird declines. *Proc. Natl Acad. Sci. USA* **101**, 18 042–18 047. (doi:10.1073/pnas.0408049101)
- 53 Ricciardi, A. & Simberloff, S. 2009 Assisted colonisation is not a viable conservation strategy. *Trends Ecol. Evol.* **24**, 248–253. (doi:10.1016/j.tree.2008.12.006)
- 54 Kaiser-Bunbury, C. N., Traveset, A. & Hansen, D. M. 2010 Conservation and restoration of plant–animal mutualisms on oceanic islands. *Perspect. Plant Ecol. Evol. Syst.* **12**, 131–143. (doi:10.1016/j.ppees.2009.10.002)
- 55 Olesen, J. M. & Valido, A. 2003 Lizards as pollinators and seed dispersers: an island phenomenon. *Trends Ecol. Evol.* **18**, 177–181. (doi:10.1016/S0169-5347(03)00004-1)
- 56 Kissling, W. D., Field, R., Korntheuer, H., Heyder, U. & Böhning-Gaese, K. 2010 Woody plants and the prediction of climate-change impacts on bird diversity. *Phil. Trans. R. Soc. B* **365**, 2035–2045. (doi:10.1098/rstb.2010.0008)
- 57 Anderson, J. T., Nuttle, T., Saldana Rojas, J. S., Pendergast, T. H. & Flecker, A. S. 2011 Extremely long-distance seed dispersal by an overfished Amazonian frugivore. *Proc. R. Soc. B* **278**, 3309–3335. (doi:10.1098/rspb.2011.0155)
- 58 Schaefer, H. M. & Schmidt, V. 2002 Feeding strategies and food intake of Blackcaps consuming ripe or unripe fruits and insects. *J. Ornithol.* **143**, 341–350. (doi:10.1046/j.1439-0361.2002.02018.x)
- 59 Menzel, A. 2003 Plant phenological anomalies in Germany and their relation to air temperature and NAO. *Clim. Change* **57**, 243–263. (doi:10.1023/A:1022880418362)
- 60 Pulido, F. & Widmer, M. 2005 Are long-distance migrants constrained in their evolutionary response to environmental change? *Ann. NY Acad. Sci.* **1046**, 228–241. (doi:10.1196/annals.1343.020)
- 61 Corlett, R. T. 2007 The impact of hunting on the mammalian fauna of tropical Asian forests. *Biotropica* **39**, 292–303. (doi:10.1111/j.1744-7429.2007.00271.x)
- 62 Hansen, D. M. & Muller, C. B. 2009 Invasive ants disrupt gecko pollination and seed dispersal of the endangered plant *Rousseia simplex* in Mauritius. *Biotropica* **41**, 202–308. (doi:10.1111/j.1744-7429.2008.00473.x)
- 63 Foster, J. T. & Robinson, S. K. 2007 Introduced birds and the fate of Hawaiian rainforests. *Conserv. Biol.* **21**, 1248–1257. (doi:10.1111/j.1523-1739.2007.00781.x)
- 64 Hansen, D. M., Kaiser, C. N. & Muller, C. B. 2008 Seed dispersal and establishment of endangered plants on oceanic islands: the Janzen–Connell model and the use of ecological analogues. *PLoS One* **3**, 1–9.
- 65 Riera, N., Traveset, A. & Garcia, O. 2004 Breakage of mutualisms by exotic species: the case of *Cneorum tricoccon* L. in the Balearic Islands (Western Mediterranean Sea). *J. Biogeogr.* **29**, 713–719. (doi:10.1046/j.1365-2699.2002.00719.x)
- 66 Traveset, A. & Riera, N. 2004 Disruption of a plant–lizard seed dispersal system and its ecological effects on a threatened endemic plant in the Balearic Islands. *Conserv. Biol.* **19**, 421–431. (doi:10.1111/j.1523-1739.2005.00019.x)
- 67 Gosper, C. R., Stansbury, C. D. & Vivian-Smith, G. 2005 Seed dispersal of fleshy-fruited invasive plants by birds: contributing factors and management options. *Divers. Distrib.* **11**, 549–558. (doi:10.1111/j.1366-9516.2005.00195.x)
- 68 Cottam, Y. H., Merton, D. V. & Wouter, H. 2006 Nutrient composition of the diet of parent-raised kakapo nestlings. *Notornis* **53**, 90–99.
- 69 Kissling, W. D., Rahbek, C. & Böhning-Gaese, K. 2007 Food plant diversity as a broad-scale determinant of avian frugivore richness. *Proc. R. Soc. B* **274**, 799–808. (doi:10.1098/rspb.2006.0311)
- 70 Seebacher, F. & Franklin, C. E. 2012 Determining environmental causes of biological effects: the need for a mechanistic physiological dimension in conservation biology. *Phil. Trans. R. Soc. B* **367**, 1607–1614. (doi:10.1098/rstb.2012.0036)
- 71 Moritz, C., Langham, G., Kearney, M., Krockenberger, A., VanDerWal, J. & Williams, S. 2012 Integrating phylogeography and physiology reveals divergence of thermal traits between central and peripheral lineages of tropical rainforest lizards. *Phil. Trans. R. Soc. B* **367**, 1680–1687. (doi:10.1098/rstb.2012.0018)
- 72 Klaassen, M., Hoyer, B. J., Nolet, B. A. & Buttemer, W. A. 2012 Ecophysiology of avian migration in the face of current global hazards. *Phil. Trans. R. Soc. B* **367**, 1719–1732. (doi:10.1098/rstb.2012.0008)
- 73 Blaustein, A. R., Gervasi, S. S., Johnson, P. T. J., Hoverman, J. T., Belden, L. K., Bradley, P. W. & Xie, G. Y. 2012 Ecophysiology meets conservation: understanding the role of disease in amphibian population declines. *Phil. Trans. R. Soc. B* **367**, 1688–1707. (doi:10.1098/rstb.2012.0011)
- 74 Brauner, C. J., Sackville, M., Gallagher, Z., Tang, S., Nendick, L. & Farrell, A. P. 2012 Physiological consequences of the salmon louse (*Lepeophtheirus salmonis*) on juvenile pink salmon (*Oncorhynchus gorbuscha*): implications for wild salmon ecology and management, and for salmon culture. *Phil. Trans. R. Soc. B* **367**, 1770–1779. (doi:10.1098/rstb.2011.0423).